

31. Contributions to the Anatomy and Systematic Arrangement of the Cestoidea. By FRANK E. BEDDARD, M.A., D.Sc., F.R.S., F.Z.S., Prosector to the Society.

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(Text-figures 72-83.)

IV. ON A SPECIES OF *INERMICAPSIFER* FROM THE HYRAX, AND ON THE GENERA *ZSCHOKKEELLA*, *THYSANOTÆNIA*, AND *HYRACOTÆNIA*.

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I obtained during the month of October 1911 a large number of fair-sized unarmed tapeworms from the gut and from the gall-bladder of an example of *Procavia capensis*, and I referred them provisionally to the genus *Zschokkeella* of Fuhrmann* in my Report to the Prosectorial Committee, in spite of the fact that the type species of that genus is a parasite of the Guinea-Fowl *Numida pitlorhyncha*. I now refer them partly to the more recently instituted genus *Inermicapsifer* †, the affinities of which with *Zschokkeella* and my own genus *Thysanotænia*, I shall deal with in the present communication. The author of the genus *Inermicapsifer*—and in the paper referred to—assigns to that genus with certainty or with more or less doubt eight species. I shall compare these individually with the species I have found myself. Dr. Janicki is certainly justified in saying that “the fact is of interest that the genus *Inermicapsifer* is parasitic in *Procavia* with several nearly related species.”

From the intestine of *Procavia capensis* I have gathered specimens of several distinct species, of which one was much more abundantly represented than the others. The more abundant species is represented in the accompanying text-figure (text-fig. 72).

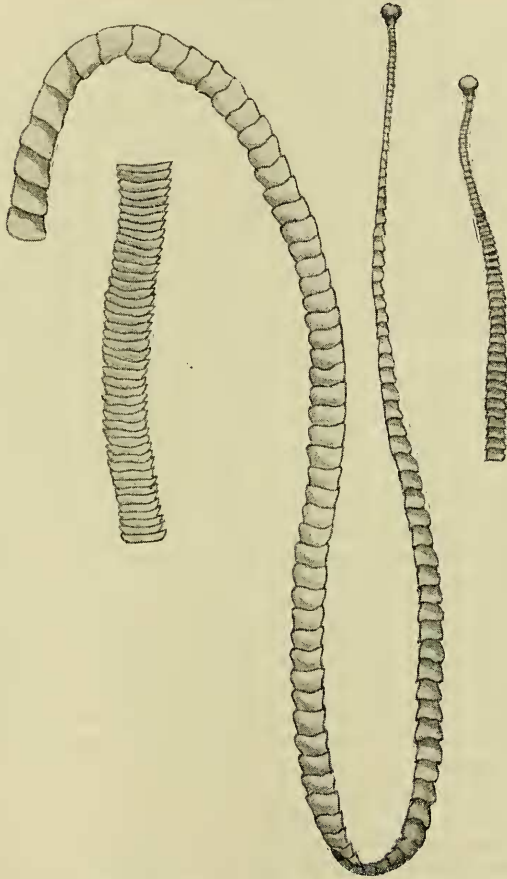
It is a long and rather slender worm, about 95 mm. in length and of 2 mm. greatest diameter. There are fully 200 proglottids in this example. The head is very conspicuous and half as wide again as the part of the strobila which ensues. Anteriorly the worm is more slender, of less diameter, than it is posteriorly; the increase is gradual, there being no sharp demarcation. The body of these worms has a great tendency in specimens preserved

* Centralbl. f. Parasit. etc. Bd. xxxii. 1902.

† Janicki, “Die Cestoden aus *Procavia*,” in Schultze’s Zool. Ergebn. Forschungsreise in Südafrika, Jena Denkschr. med. Ges. xvi., 1910.

in alcohol to contract upwards or downwards, thus forming a hollow or convex surface as the case may be. The characters already given allow us to separate the present species from *I. hyracis**, in which the scolex is not of greater diameter than the ensuing region of the strobila, and from *I. settii*†, where the total number of proglottids is very small (*i. e.* 30-70).

Text-fig. 72.



A nearly complete example and two fragments of *Inermicapsifer capensis*.
× 2.

I do not at this stage of my description attempt to differentiate between this species and the others dealt with in Janicki's

* Janicki, *loc. cit.* pl. xii. fig. 1.

† Janicki, *loc. cit.* pl. xii. fig. 10.

monograph, since there is some little variation in the characters of the numerous examples which I have to consider here, which variations do not militate against the exclusion of *I. hyracis* and *I. settii*, though they render difficult the distinguishing of my species from some of the others referred to by Janicki. Thus two examples measured only 68 mm. and 75 mm. respectively, and one of them was quite 3 mm. in diameter at the widest part. The segments were never longer than broad, except perhaps a trifle longer in the thin anterior region of the body. They varied somewhat in relative dimensions, as is the case* with those of *I. hyracis*. Occasionally the unilateral genital pores were very visible on slight papillæ near to the hinder end of segments.

The *scolex* is quite unarmed and conspicuous by its size, as already mentioned. It is usually more or less globular in form, with a slightly prominent and somewhat pointed apex, as is shown in Janicki's figure of *I. settii* †, and which is, of course, the rostellar region. Occasionally, however, this apical region does not protrude, but is represented by a depression on the surface. The *scolex* is, moreover, sometimes flattened in its entirety from above downwards, and presents a mushroom-like appearance, the edges of the disc projecting round the neck, which thus presents the appearance of the stalk of the mushroom.

Longitudinal sections through the *scolex* confirm the total absence of hooks or of any trace of a rostellum, save the slight projection already mentioned. Nor could I detect anything peculiar in the structure of the suckers, which, according to Janicki and others, are remarkable for a funnel-like ingrowth leading to the actual sucker, which thus lies at the bottom of a depression. It is true that in the present species, as in many tapeworms of the group Tetracotylea which I have examined, the sucker does not lie externally on the *scolex*, but is covered by an outer layer of body-wall which is only interrupted at the orifice of the sucker. The free edge of this, when depressed towards the interior of the sucker, is doubtless funnel-shaped and would give rise to the appearances represented by Janicki. Perhaps, however, there is some divergence from the normal condition of the suckers in the members of the genus referred to by him, which I certainly have not found in the species with which I am at present concerned. The direction of the suckers seems to me to vary somewhat; generally they are lateral, but sometimes with a forward inclination.

It has been already observed that in this genus water-vessels of unusual width extend far into the head. Such are figured by Janicki, and referred to by Pagenstecher ‡ (quoted by Janicki §) as "einen mit Ringmuskeln umspinnenen Wasserbehälter." In

* Janicki, *loc. cit.* pl. xii. figs. 2-5.

† *Loc. cit.* pl. xii. fig. 10.

‡ Zeitschr. f. wiss. Zool. Bd. xxx. 1878.

§ *Loc. cit.* p. 389.

the present species a good deal of the head lying between the suckers is occupied by the coils of water-tubes, which approach very nearly to the external surface at the apex of the head. These tubes are not in any way irregularly dilated, but their diameter throughout is rather greater than that of the tubes in the immediately following neck-region of the body. Janicki is not disposed to lay great weight upon the absence or presence of a neck in these tapeworms. In the present form the strobilisations begin very close to the head, which is supported by a segment broadening towards the head, which may be regarded as the neck. In the accompanying text-figure (text-fig. 72) will be seen the general characters of the strobila of this worm.

The body-wall of the worm is relatively thick, but here the cortical layer is not so definitely marked off from the medullary parenchyma as is so often the case. The absence of a strong delimitation is due to the very feeble development of the transverse musculature, which is generally hardly, or not at all, recognisable in transverse sections. Another reason which renders the two layers more uniform in this species than in my *Thysanotenia gambiana* and in the species of *Hyracotænia* described in the present paper, is that there are stout muscular fibres in the medullary parenchyma comparable in thickness to the longitudinal muscular fibres of the cortical layer.

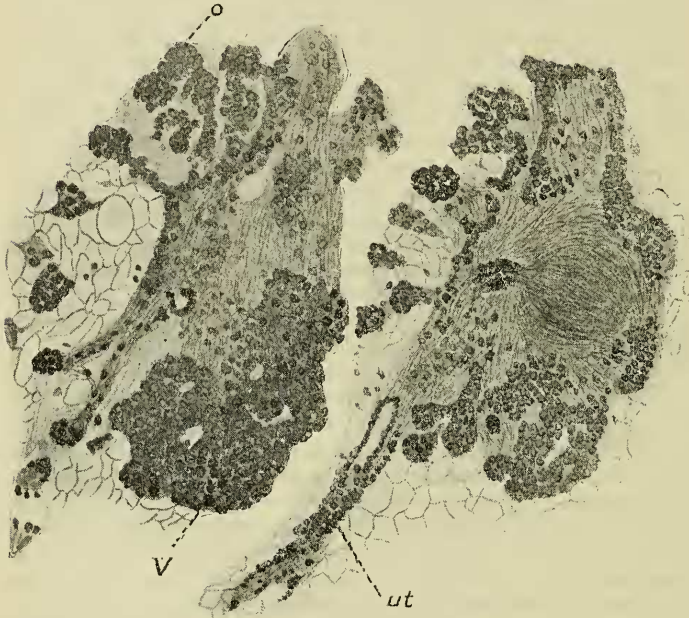
Water Vascular Tubes.—These tubes are, as usual, two on each side. They lie, as a rule, almost parallel with each other, the smaller dorsal tube having, however, an inclination to the dorsal side which is more or less pronounced as the case may be. The more medianly situate ventral tube is the wider, but the difference between the two is not perhaps quite so well-marked as in *Thysanotenia gambiana*. The two vessels are not united across the proglottids by a regular series of transverse vessels, one to each proglottid, but, as in other species of this genus and in *Thysanotænia gambiana*, are united by a network of tubes found all over the segments. I did not follow out into any detail the precise arrangement of the branching connecting-tubes.

The *ovary*, when fully mature, appears to be definitely a single body lying anterior to and in contact with the vitelline gland. The latter lies on a level with the group of testes of the pore side. The ovary lies, when less fully mature, entirely to the median side of the two water vascular tubes. Later on, it appears to extend somewhat and is larger actually, and considerably larger relatively, than I found it to be in *Thysanotenia gambiana*. The ovary is clearly also larger in the present species than in *Inermicapsifer hyracis*, according to Janicki's figures. In the later stages of the ovary, when it is gorged with ripe eggs and these are beginning to spread through the proglottid, a peculiarity of structure, perfectly plain in earlier stages, is not obvious. One such example, representing the ovaries, is represented in text-figs. 73 and 74. It will be there seen that the ovary really consists of clumps of ripe and unripe eggs situated at the ends of

stalk-like processes of the oviduct, from which they radiate out. There is some evidence that these are probably hollow outgrowths of the oviduct, the main stem of which is continued on to form the rudimentary (at any rate, short) uterus. There is also some evidence that these outgrowths of the oviducal canal form here and there anastomoses with each other. In the fully mature ovary the ripe eggs are seen to be in groups surrounded by a thin wall and with empty spaces surrounding eggs or groups of eggs.

Text-fig. 73.

Text-fig. 74.

Text-fig. 73.—Ovary and vitelline gland of *Inernicapsifer capensis* in section.

o. Ovary. *V.* Vitelline gland.

The masses of ova are seen at the end of stalk-like processes.

Text-fig. 74.—Another section through the same ovary to show the rudimentary uterus (*ut.*).

It seems to me that we have here a later stage of the tubes communicating with the oviduct. From this point of view the ovary would appear to be a compound body, in reality consisting of many ovaries; the indications of a network among these ducts is particularly interesting in view of the network formed by the testicular ducts, and brings the male and female organs into closer agreement.

The *vagina* opens on the exterior behind the aperture of the cirrus sac and immediately contiguous to it. As will be mentioned in describing the cirrus sac there is no common cloaca. The direction of the tube from its opening into the receptaculum seminis is obliquely backward, the external pore lying at the side of the segment posteriorly. The terminal portion of the vagina, the length of which is not far from equal to that of the cirrus sac, is somewhat dilated and with a wider lumen; it is plainly ciliated. The whole of the vagina is very muscular, the muscular layer being as thick as that of the cirrus sac. The lining epithelium is deeply stained. The course of the vagina is very straight until it bends somewhat at its entrance into the large receptaculum seminis. The latter is bent round the outermost of the two longitudinal water vessels. From its opposite end arises the wide common duct, which after a short course divides into the posterior vitelline duct and the anterior oviduct. The two latter are in the same straight line.

A closer examination, however, of the long muscular vagina shows that it is really divisible into two regions. These are inequized, the larger section being that which is nearer to the external pore. This section has a much wider lumen than the ensuing section, which opens into the wide and thin-walled oviduct. The latter has a narrow thread-like lumen, but still thick and muscular walls. It is not so long as the distal region of the vagina. This part corresponds to the very short and suddenly abbreviated part of the vagina in *Thysanotenia gambiana*; but is obviously very much more developed. It is not in the same straight line as the wider distal section of the vagina, but bends back to meet the forwardly running oviduct. This division of the vagina appears to be very characteristic of the present species.

At the time that I was preparing my account of the anatomy of the two species of my genus *Thysanotenia* I was not acquainted with Janicki's memoir upon his genus *Inermicapsifer*, and therefore laid no stress upon some structural features which are of importance in comparing these forms. I have therefore carefully re-examined my sections of *Thysanotenia gambiana*, and made in addition several series of fresh sections, in order the better to accomplish this comparison. By these means I am in a position to make a few corrections in, and additions to, my earlier account.

I find that account, however, to be correct in all essentials, excepting with regard to the presence of a vesicula seminalis in the neighbourhood of the ovary. This was doubtfully asserted, however, and I now find that the structure in question is really a part of the dilated and thin-walled oviduct, which runs straight, as I have said, from the thick-walled region near to the external pore and gradually increases somewhat in width as it approaches the ovary. I confirm my account of the variability in the lateral extension of the ovary and vitelline gland, which

are sometimes restricted in their extent to the space lying between the dorsal and ventral vessels. In incompletely mature proglottids this restriction appeared to be (at least usually) the case, the gonadial tissue not extending outside or inside of the two excretory tubes. I should also emphasize the fact that the ovary and vitelline glands are, at least for part of their extent, situated side by side. That is to say, the vitelline gland is not wholly behind the ovary. In young proglottids the general lie of the female gonad seemed to me to be rather oblique dorso-ventrally, in accordance with the fact that the duct passes to the exterior ventrally of the dorsal excretory vessel and that the two excretory vessels lie in a nearly parallel plane.

I have also a new fact of some little importance to add. I have described the uterus in the sexually mature segments as being a tubular structure running across the segments. I have in younger specimens discovered the rudimentary uterus, which consists of a solid chord of closely packed cells which enclose no lumen. This is connected with the gonad tissue lying between the two excretory tubes and passes towards, but not far towards, the middle line of the body above the larger ventral excretory tube, but below the sperm-duct. The rudimentary uterus ends in a club-shaped blind extremity.

My former account of the testes of *Thysanotenia gambiana* is confirmed by the examination of fresh material. I have, however, two points to add: the first is that while the testes are practically grouped as there stated into two groups, there are, nevertheless, a very few testes lying between the two ventral excretory tubes, and thus really constituting a bridge between the two separate masses, and bringing the arrangement of the testes more into line with that of the second species of the genus *Thysanotenia* described in the paper referred to. These, however, are indeed few; I counted but three in a single proglottid. The general statement with regard to the testes remains, therefore, unaffected. Moreover, each testis is rounded or oval in form, but I could not find the distinctly pear-shaped outline that I describe in the species of *Inermicapsifer* dealt with in the present paper. I should, furthermore, add to my former account the fact that the testes are mature before the ovaries, and that in segments where the ovary is still immature the vagina, as well as the vas deferens, is filled with sperm. The sperm-duct is coiled and the coil lies principally between the nerve-chord and the dorsal excretory tube, extending to a short distance medial of the latter. The coils have some regularity and lie dorso-ventrally and parallel. I have found granular tissue accompanying the sperm-duct. Cells lay here and there between the coils, sometimes in numbers.

The testes of the worm from the Hyrax are very distinctly arranged in two sets in each proglottid. The great bulk of these organs are on the side furthest away from the external pore. I did not find a few scattered testes uniting these two groups such as occur

in *Thysanotenia gambiana*. The point of difference, however, is not a large one, since in other species of the present genus there is no differentiation of the testes into two masses, but they form a continuous mass reaching from side to side of the proglottid. In the case of the group of testes on the pore side, they lie to the pore side of the ovary and vitelline gland. These testes were very conspicuously pear-shaped, the duct naturally arising from the pointed end. In the case of the testes on the pore side, at any rate, the narrower end faced forwards in the segment. In the case of each group the testes are closely packed together. They are restricted to the medullary part of the parenchyma. The efferent sperm-ducts from the testes which lie away from the pore side form a widish trunk which breaks off and forms a slight rete mirabile not so marked as in the species next to be described. This opens evidently by one thick tube into the large vesicula seminalis lying close to the ovary and to the receptaculum seminis.

The *cirrus sac* is not conspicuously large, and it lies close to the lateral margin of each proglottid and thus well within the cortical parenchyma. Its position is oblique, the end of the sac being anterior to its aperture on to the exterior, and is thus better shown in horizontal than transverse sections of the proglottids. The general outline of the cirrus sac, when displayed in such sections, is, like that of many other species (e. g. *Otiditenia eupodotidis**), flask-shaped, there being a narrower proximal neck and a wider distal region. It lies parallel to the vagina and very close to it, but in a different plane, so that a single horizontal section does not display both tubes lying side by side. Such a section, however, does show the extreme terminal part including the external orifice of both cirrus sac and vagina; and it will be seen that they lie accurately side by side, the male pore being, of course, anterior to the female pore. Such a section also shows very plainly that there is no trace of a cloaca genitalis; the two pores are upon the surface of the body upon a slightly raised papilla of not very great dimensions. The papilla which bears the two orifices is clearly of less importance than that which characterises the two worms for which I have recently formed the genus *Thysanotenia* †. On a re-examination of my sections of the species *Thysanotenia lemuris* I find that in that species, as well as in that which forms the subject of the present communication, there is no sinus genitalis, but that both cirrus sac and vagina open side by side on the summit of the papilla. The case is otherwise with *Thysanotenia gambiana*, where there is a distinct though not very large sinus or cloaca genitalis. There are also corresponding differences in the vagina and cirrus sac of the latter, which I shall deal with after describing the arrangements found in the Anoplocephalid from the Hyrax.

The cirrus sac has a thickish muscular coat which does not become at all markedly thicker in the "neck" region. In

* P. Z. S. 1912, p. 206, text-fig. 27.

† P. Z. S. 1911, p. 1002.

longitudinal sections it appears that the fibres constituting together this muscular wall run more or less along its longer axis. It will be observed that in both of these characters the cirrus sac of this species differs from that of a genus recently described by myself as *Otiditenia**, and, moreover, the cirrus sac is very much larger in the latter genus. The cirrus itself is very inconspicuous and occupies only the neck region of the sac; it is thus necessarily very short. It is distinguishable from the sperm-duct by reason of the fact that it is very darkly stained with both carmine and hæmatoxylin. Between the cirrus and the muscular walls of that part of the cirrus sac in which it lies is a great accumulation of nuclei, which belong, as I presume, to slender muscular fibres concerned with the retraction of the cirrus.

As in other species the cirrus sac, where it swells out into the rounded flask-like body, is filled with a delicate packing tissue with abundant nuclei. Through this passes the sperm-duct in two or three coils. The delicate sperm-duct takes up but little stain and is thus very distinct from the cirrus. I found this condition of the sperm-duct to exist in a segment *posterior* to others in which the sperm-duct had undergone even further modification. In the latter segments the sperm-duct lying within the cirrus sac is dilated to form a vesicula seminalis. This dilated duct is also coiled; but the two or at most three pieces seen in an individual section completely fill the lumen of the cirrus sac, with the exception of dividing lines filled with nuclei belonging to the internal tissue of the cirrus sac. The fact that an unaltered sperm-duct may lie behind one which is converted into a vesicula seminalis is important.

It is clear that, on the whole, the cirrus sac of this worm is more like that of the two species which I have referred to a new genus, *Thysanotenia*, than it is to that of, for example, *Otiditenia*† or *Anoplolenia*‡. It differs, however, in details from the cirrus sac of both of the two species which I have temporarily placed in the genus *Thysanotenia*. In the concluding part of the present communication it will be necessary to go fully into the systematic position of this worm and to compare it especially with the two species of the genus *Thysanotenia*. It will be therefore convenient at the present moment to compare the cirrus sac in these different forms. They agree generally in the absence of a distal region, which I have termed penis in *Anoplolenia*, the cirrus being rod-like up to its free extremity and not lying at the bottom of an invaginated part of the cloaca genitalis. Again, in all three species the general form is the same, and the muscular layer runs along the longer diameter of the sac and is not specially thickened at the "neck" end. These features exhaust the general resemblances between the

* P. Z. S. 1912, p. 206, text-fig. 27.

† P. Z. S. 1912, p. 194.

‡ P. Z. S. 1911, p. 1015, text-fig. 215.

cirrus sacs of the three tapeworms. That of *Thysanotenia lemuris* differs from the other two by its larger size, the cirrus sac in the two remaining species being of about the same size. The cirrus sac of *Thysanotenia lemuris* is, indeed, fully twice the size that it is in the two other species. In the species which forms the subject of the present communication the cirrus is very small and limited to the neck part of the cirrus sac, than which it is no longer. The same characteristics apply to *Thysanotenia lemuris*, only that as the cirrus sac itself is larger, the cirrus also is larger than that of the species with which I compare it. In both of these species the rest of the cirrus sac is filled with the sperm-duct, which is, in both, dilated to form a vesicula seminalis; but in *Thysanotenia lemuris* the dilatation fills the whole sac, while in the other species it is coiled and thus fills the sac in a different way. In the species *Thysanotenia gambiana* there is no such conspicuous vesicula seminalis, but just after the entry of the sperm-duct into the cirrus sac it is dilated for a short space. On the whole, it appears that the cirrus sac of the present species is more like that of *Thysanotenia lemuris* than of *Th. gambiana*.

One of the principal differences which this species shows from *Thysanotenia gambiana* is in the character of the uterus. As I have already mentioned in the present paper, as well as in my memoir dealing with that species, the uterus is very plain, first as a solid cord and then a narrow tube with an obvious lumen. An examination of a large number of sections of the species of *Inermicapsifer* described here has shown nothing exactly like the uterus of *Thysanotenia gambiana*. Nor can I reconcile what I have seen with the figures of Janicki's illustration of the uterus of *Inermicapsifer hyracis*. In the latter species the uterus is figured* in horizontal sections through the ripe proglottid as an irregularly shaped sac with numerous projections and outpushings of its lumen—as, for example, in the genus *Tetrabothrium* †. It is shown, however ‡, to commence as a sinuous tubular structure, which appears to me to resemble very much the uterus as I have described it in *Thysanotenia gambiana*. Earlier still than this a solid cord of cells issues from the generative mass which again would appear to be exactly comparable to what I have seen in *Thysanotenia gambiana*. Janicki, however, comments upon the remarkable fact that the formation of a lumen in this cord begins, not where it would be expected to begin, at the ovarian end, but towards the middle of the segment. It is here, moreover, that in *Thysanotenia gambiana* the solid cord of cells, which subsequently becomes the hollow uterus, widens out into a club-shaped extremity; but I am unable to confirm or differ from Janicki in fixing the point at which the uterus begins to be hollowed out to be coincident with this club-shaped extremity. It seems, however, to be very likely.

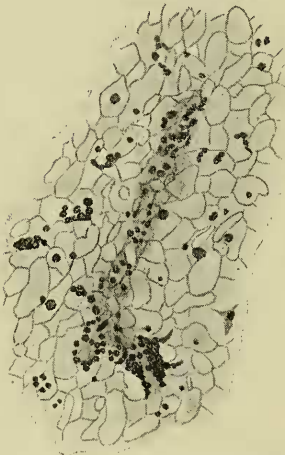
* *Loc. cit.* pl. xii. fig. 13.

† Spätlich, in *Zool. Jahrb.* Bd. 28 (1909).

‡ *Loc. cit.* pl. xii. fig. 17, ut.

The examination of more than one series of sections has shown me that, in the species of *Inermicapsifer* which forms the subject of the present communication, the commencement of the formation of the uterus is in many respects different from that of *Inermicapsifer hyracis* as described by Janicki and of *Thysanotenia gambiana* as described by myself. The earliest stages that I have observed are perhaps best seen in horizontal sections, though I have also observed them in transverse sections. In horizontal sections, such as is represented in text-fig. 74, the ovary lies in the middle of the segment from before behind and extends some way towards the middle of the segment from right to left. The oviduct with its numerous branches, which has been

Text-fig. 75.



Text-fig. 76.



Text-fig. 75.—A portion of the medullary parenchyma of *Inermicapsifer capensis*, showing centrally a condensation of tissue which is connected with the rudimentary uterus.

Text-fig. 76.—A portion of the ovary of the same species with eggs (o) detached from the ovary and lying in the parenchyma, and a portion of the network of tissue (x) which may possibly represent the uterus.

already described, is seen to be prolonged into an extension not distinguishable from it, which runs for a little way into the medullary parenchyma towards the median point of the proglottid. It is quite short, and ends more or less abruptly in a strand of condensed parenchymal tissue, which is apt to be branched, sending out shorter strands of a similar appearance in an oblique direction. Some of these ceased after a short course. In neighbouring regions of the proglottid (text-figs. 75 and 76) there were patches or rather strand-like parts of the medullary parenchyma

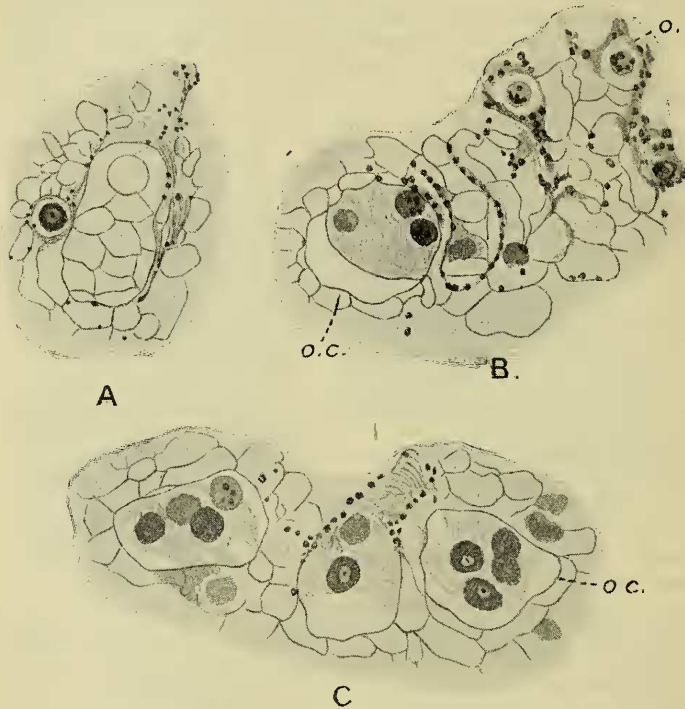
exactly similar to those which have been described as continuous with the prolonged oviduct, but not always continuous with it. They would seem to be produced independently of the generative ducts. A network arrangement often characterised these regions of the medullary parenchyma. This condition of the uterus characterised proglottids in the same stage of evolution as those which in *Thysanotenia gambiana* possessed an uterus with a distinct lumen. But if we are to compare them with earlier proglottids in *Thysanotenia*, then it must be remarked that in the present species of *Inermicapsifer* there is no such regular band of nuclei, marking out the future uterus, as exists in the former worm. The appearance is, in fact, totally different. In *Inermicapsifer* the suggestion is merely of a crowding together in a quite irregular fashion and a local multiplication of the nuclei of the cells of the medullary parenchyma. In *Thysanotenia* the nuclei are in orderly arrangement and regular sequence, obviously belonging to an organ which, as already pointed out, swells at its medianly situate end into an oval region of greater diameter. In *Thysanotenia* we have obviously a regular outgrowth of the generative system; in my species of *Inermicapsifer* what would appear to be a condensation of parenchymal tissue in contact with and continuing on a very short, and in this species hollow, outgrowth of the generative duct. I am not clear whether the species described by Janicki agrees most nearly with the species described in the present paper or with *Thysanotenia gambiana*. I am disposed to think that the branched strand in which the slightly prolonged oviduct ends in this *Inermicapsifer* is not the homologue of the solid mass of cells in *Thysanotenia gambiana*, which afterwards becomes hollowed out to form the uterus of that worm; in this case *Inermicapsifer hyracis* agrees more closely with *Thysanotenia gambiana* than with the species described here.

It might possibly be held that this network, which permeates the segment when seen in horizontal section, is merely a stage subsequent to that figured by Janicki in a proglottid of somewhere near the same stage of maturity as that which I am now considering in the species of *Inermicapsifer* studied by myself—that the lumen had, in fact, existed and had disappeared. That this is not the case is clear from the fact that in this stage there were not any ova contained in the meshwork, and in fact no ripe ova anywhere outside of the ovary. The meshwork formed by condensation of the parenchyma, in fact, precedes the extrusion of ova from the ovary. Still, it may represent the imperfect remains of a retiform uterus such as is characteristic of the genus *Dipylidium* or, better perhaps, in relation to the present genus, the Anoplocephalid genus *Andrya*.

I have also been able to approach the question of the identity or non-identity of the cavity in which the eggs lie with the cavity of the uterus from another side. Text-fig. 77 represents portions of horizontal sections through a proglottid in which the

eggs are leaving the ovary to be scattered through the medullary parenchyma, though in this particular stage the whole parenchyma is not filled with eggs as it is later and at the end when the whole medullary region is crammed with the paruterine organs. As will be seen by a reference to the figures cited, the eggs lie partly in round or oval cavities which might well be

Text-fig. 77.



Three sections through the medullary tissue in the neighbourhood of the ovary of *Inermicapsifer capensis*.

In **A** a single ovum is shown to the left. In the centre is an oval area with strongly marked walls, but filled with the ordinary medullary tissue.

B shows eggs (*o.*) lying each in a single vesicle of the medullary tissue and three eggs lying in a cavity (*o.e.*).

C. Three of the cavities (*o.e.*) containing eggs and also showing remains of the medullary tissue which is shown unaltered in **A**.

thought to be uterine cavities were no further information forthcoming. I believe, however, that these cavities are not remnants of a uterus, as is held by Janicki to be the case with apparently similar cavities in *Inermicapsifer hyracis*. A close

examination of the cavities seems to show that they are lined by a flattened epithelium, of which the nuclei are apparent and are represented in the figure, and there is a slight accentuation of the wall of the cavity, which is merely, as I think, the portion of the parenchymatous network which abuts upon the cavity and is not a special layer distinct from that; in this case the apparent lining epithelium should be regarded merely as the nuclei belonging to this part of the parenchymatous network. I believe this to be the real explanation; for when we look carefully into the cavity itself, in which eggs lie in various numbers, there is nearly always, if not quite always, some granular detritus to be seen and which is shown in the figures referred to. This formless detritus (as it often, but not always, is) might, of course, be interpreted as simply coagulated fluid which it would not be surprising to meet with in the interior of a uterus were this system of cavities the remains of a uterus. But, as will be seen, this detritus is susceptible of another explanation; it is, as I think, the remains of the delicate parenchymal network originally present, as is shown in text-fig. 77 A, in these regions of the parenchyma set apart for the development of the eggs. The figure referred to shows plainly an area oval in section and with a slightly accentuated wall, marking it off from the surrounding tissue, which is filled with parenchyma network, but does not as yet contain any eggs. If my contention is right, then it must follow that the space containing developing eggs is at least not always to be referred to a uterus. Nor is it in the least against this view that it is possible to meet with these circular spaces in which nothing is apparent but eggs—that is to say, no remains of the originally present parenchymal network, for this may have completely disappeared. I would furthermore point out that the position of the eggs in the nearly empty cavity shown in text-fig. 77 B suggests that they have only just forced themselves into the cavity.

I have yet another argument to show reason against regarding the cavities of the paruterine organs in which the embryos are finally lodged as detached fragments of the pre-existing uterus; or, at any rate, to show that they cannot always be so regarded. In text-fig. 77 B and text-fig. 76 is represented an ovum lodged in one of the meshes of the parenchymatous network of the medullary region without any special relation to the larger egg-containing cavities which have been looked upon as detached fragments of a uterus. There are plenty of such examples to be seen in sections of this age, and it is plain to me that eggs are constantly lodged singly in the parenchymal network. I argue this from the fact that in these cases the cavities lodging the eggs are in every way indistinguishable in size and appearance from the cavities of the parenchyma in which an egg is not lodged. It may be, of course, that these are eggs which got extruded from a uterine cavity and forced into the surrounding parenchymatous network. But it is equally reasonable

to assume that they have got directly to their situation from the ovary (see text-fig. 76). The lax parenchymal tissue, the mesh-work of which is filled with a substance plainly visible as granular matter after staining with Ehrlich's hæmatoxylin, but not to be seen after staining with borax carmine, can offer little obstacle to the immigration of eggs; so that in any case some of the paruterine organs are without vestiges of an uterine cavity. I believe, as a matter of fact, that all are so, and that there is no persistent uterus in this worm.

The *paruterine organs* of this species resemble those of the species which I described as *Thysanotœnia**. At the time when that description was written, I believe that Janicki's careful account of the genus *Inermicapsifer* with similar egg-capsules had not actually appeared. I had not realised from the descriptions of *Zschokkeella* that the organs containing the ripe eggs were doubtless of the same structure. I had considered that those organs probably resembled the figure given by Ransom †, not entirely grasping the fact that that figure was intended rather as a diagram to distinguish between those species of *Davainea* which had several eggs enclosed in one capsule and those species in which each capsule had within it but one egg. I was thus misled, though not through Mr. Ransom's fault. There was, of course, no other genus with which I could directly compare *Thysanotœnia gambiana*.

In defining the genus *Zschokkeella*, Ransom speaks of the fate of the uterus in the following words:—"Uterus early breaks down into egg-capsules." Earlier in his résumé, Ransom defines the subfamily Linstowinæ in the same way; he remarks that the "uterus breaks down into egg-capsules." As the subfamily Thysanosominae is defined by the presence (*inter alia*) of numerous paruterine organs, I thought myself justified in placing my genus, as I regarded it, in the latter subfamily and marked its affinities by the use of the generic name *Thysanotœnia*. I was indeed of opinion that the uterus in *Zschokkeella* really persisted in separate pieces, each containing so many eggs. It appeared to me, in fact, after studying a tapeworm which I have lately described in the 'Proceedings' of this Society as *Otiditœnia* ‡, that the fate of the uterus in *Zschokkeella* might be like that of *Otiditœnia*. No figures are given by Fuhrmann in his account of *Zschokkeella linstowi* § which illustrate this particular point, and the only reference to the matter is the assertion that the eggs are surrounded by a "Parenchymhülle."

Janicki ||, however, is apparently of my earlier opinion; for, in distinguishing between the genus *Zschokkeella* (written, as originally—*Zschokkea*) of Fuhrmann and his own genus

* P. Z. S. 1911, p. 1001.

† Bull. U.S. Nat. Mus. No. 69, 1909, p. 17, fig. 8.

‡ P. Z. S. 1912, p. 194.

§ Centralbl. f. Bakt. u. Paras. Bd. xxxii. (1902).

|| *Loc. cit.* p. 393.

Inermicapsifer, he uses the differences between the egg-capsules in the two genera. He considers that in *Zschokkeella* the eggs lie "einzeln in einfache Bindegewebskapseln," a difference which also appeared to me to hold good. I do not, however, feel confident about this point, and in view of other points of likeness between the genera am disposed to compare more nearly the paruterine organs in the two. In my paper upon *Otiditenia* just referred to I have dealt to some extent with the "egg-capsules" of *Davainea*, of which the various figures published are not quite in unison. I find a justification for this in the paruterine organs of *Inermicapsifer capensis*, where the appearances vary slightly among examples which I cannot refer to different species.

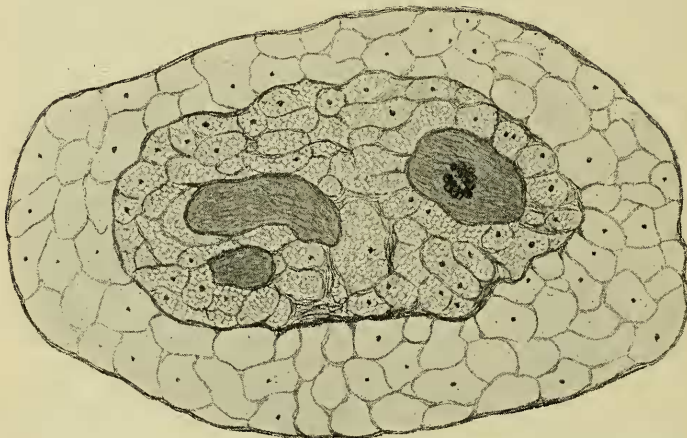
To begin with, I prefer the name of paruterine organs for the structures in question, because they seem to me to be exactly comparable to structures so named in other tapeworms. They are, in fact, sacs formed out of the parenchymal tissue, whether they have or have not ultimately a connection with the uterus. I should prefer to term the egg-containing spaces in *Otiditenia* "egg-sacs" which are formed in a different way, *i. e.* by a breaking up of the uterus. When specimens of this *Inermicapsifer* were examined alive in salt-solution, the individual paruterine organs could easily be squeezed out of the body by crushing it. They were then spherical or egg-shaped and appeared to be surrounded by a thick, colourless, and almost structureless membrane. This membrane exhibited only faint striæ in a longitudinal direction, being thus concentric in reference to the whole body. The interior was filled with quite transparent spherical embryos, between which were abundant cells with granular contents.

In stained preparations (text-fig. 78) the outer layer was also perfectly distinguishable. It was stained more lightly than the inner by carmine and more deeply by logwood. A figure of the mature organ in *Inermicapsifer hyracis* is given by Janicki *, with which may be compared my own figure of the same organ in the species described here. The appearances shown by the organ in the living condition are not borne out by preserved and stained material. The outer layer is not fibrous but cellular, as shown by Janicki and others. This layer is, however, as a rule, quite distinct from the inner mass of cells immediately surrounding the embryos. The distinction between the two partly depends, as already mentioned, upon stains, and is not always obvious. I do not see in my specimens of *Inermicapsifer capensis* so great a distinction between the outer and inner cells in point of size and shape as does Dr. Janicki, which is perhaps rather remarkable in consideration of the very different appearances they present when living. The cells of both layers are, in fact, rounded and nucleated, and not greatly different in size and shape. Those of the inner layer are filled with larger spherules. They are

* *Loc. cit.* pl. xiv. fig. 28.

separated by a more deeply staining reticulum, which appears to be similar to that of the general parenchyma. This forms a somewhat thicker layer enclosing the whole organ. The reticulum of the inner mass of cells is thicker than that of the outer layer, and the nuclei lying at intervals along its strands are very obvious. The reticulum also forms a distinct layer separating the outer from the inner mass of cells. In fact, the whole organ is of an appearance more like that represented by Fuhrmann* for *Davainea* than that by Janicki. This is so, at any rate, as regards the outer layer. The interstitial substance of the inner mass of cells forming the reticulum is represented by Janicki, but as of much greater relative extent than I have found it.

Text-fig. 78.



Paruterine organ of *Inermicapsifer capensis*, showing differentiation between outer and inner coat.

The species that has just been described cannot, as I think, be referred to any of those enumerated by Janicki. It differs from *I. hyracis* in the form of the scolex, in the fact that the testes are arranged in two separate masses in each proglottid instead of forming a continuous row. From *I. interpositus* my species differs also in the arrangement of the testes, and in the fact that the genital pores of *I. interpositus* are anterior in position and open into a well-marked cloaca, and also in the fact that the sexual products are ripe earlier in the body in *I. interpositus*.

Nor can *I. settii* be confused with my species. For in the former the body is very short and consists of not more than 70 proglottids. Moreover, the excretory vessels do not approach

* Rev. Zool. Suisse, iv. (1896).

so nearly to the apex of the scolex, nor are they so coiled in that region as in my species. On the other hand, the two species agree in the posterior position of the genital pores and the separation of the testes into two masses. There may be a difference also in the lack of an excretory network in *I. settii*, of the existence of which Janicki is not certain.

There remain certain less-known species referred by Janicki to the genus *Inermicapsifer* with more or less certainty and of whose characters he gives some account. Of these, "*Tenia paronai*" cannot be identical with my species, since it possesses hooks; "*Tenia spatula*" of von Linstow is too imperfectly described to admit of its definite inclusion in the genus *Inermicapsifer*. It cannot, however, be identical with my species, since the cirrus sac is apparently much larger ("Der Cirrusbeutel nimmt 1/7 des Querdurchmessers ein") and the testes are scattered through the greater part of the segment. *Tenia ghondhorensis* of Klaptocz is very imperfectly known, but a pit upon the scolex shows that it is not identical with my species.

From *I. criticus* of Pagenstecher (which is perhaps identical with another species described below), the present species can be distinguished by the grouping of the testes into two masses.

I. pagenstecheri of Setti differs from my species by its few proglottids (not more than 80); otherwise it seems to present more resemblances to my species than any other form except *I. settii* by virtue of the posterior position of the genital pores.

To a species termed by Nassonov *Anoplocephala hyracis* Rud. var. *hepatica*, and by Janicki "*Inermicapsifer* spec.?" I shall recur in considering some worms from the gall-bladder of *Procavia capensis*. In the meantime my own species may be thus defined and named:—

Inermicapsifer capensis, sp. n.

Length about 95 mm., *breadth* 2 mm.; *number of proglottids* 200. *Scolex* wider than the neck. *Proglottids* at end of body nearly as long as wide. *Genital pores* unilateral near to posterior end of proglottids, not borne upon a conspicuous projection. *Testes* in two separate groups, one on pore side and one on opposite side of proglottid. *Vas deferens* forms a network; a large *vesicula seminalis* present; *cirrus sac* small, filled with slightly coiled and dilated sperm-duct. *Uterus* short and not persistent. *Many paruterine organs*, each containing several embryos.

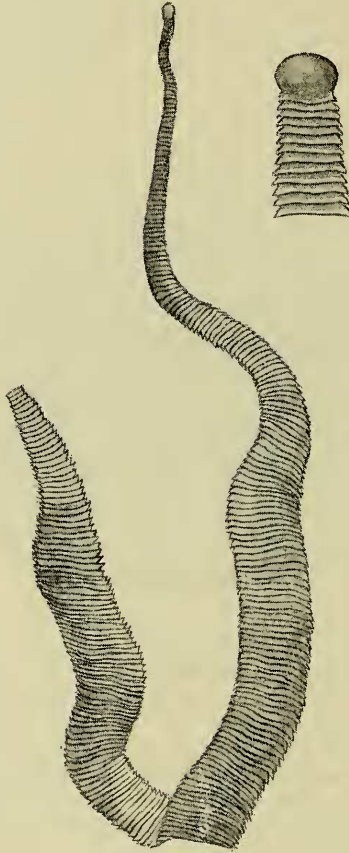
Hab. *Procavia capensis*.

On Species of the Genus Hyracotænia, gen. nov.

Along with the numerous examples of the tapeworm which I have described here as *Inermicapsifer capensis*, I found in the gut of the Hyrax two complete or nearly complete examples of a tapeworm which has quite a different external appearance, and whose

internal structure is different from that of the former species. Before examining it anatomically it was, of course, impossible to say whether or no these worms belonged to the genus referred to, and even now it is possible that they may be of the same species as one or more of those which Janicki has—provisionally, at any rate,—assigned to the genus *Inermicapsifer*. They are, however,

Text-fig. 79.

*Hyracotænia hyracis.* × 2.

clearly not members of that genus, as the following account of their structure will prove. Nor can I, with any confidence, refer them to any other known genus. Hence I propose the above name, which is indicative of their habitat. I shall enquire later as to

the possibility of their identity with any other species known from the Hyrax. The two worms belong, as I think, to two different species, but are referable to the same genus without any doubt. I shall consider the anatomy of both of them together.

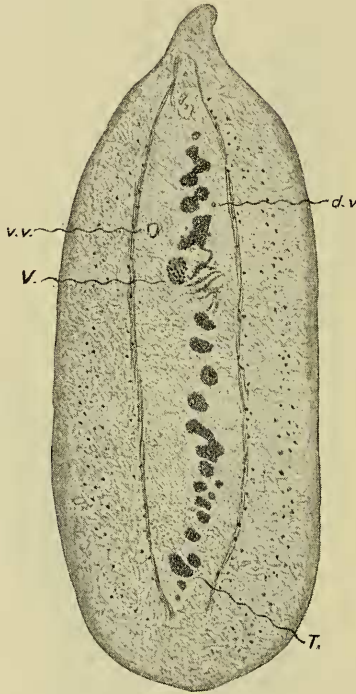
The larger specimen (text-fig. 79) measured about 90 mm. in length by a greatest diameter of 5-6 mm. The proglottids are very short in an antero-posterior direction, but, at any rate some way back in the body, rather thick. If there is a neck present at all it is very short. The scolex is unarmed and distinctly marked off from the strobila, but not much wider than the ensuing body. The latter increases gradually in width up to the widest point, and towards the end of the body again decreases. Of the smaller specimen I cannot give such precise details, since, believing at first that both specimens were of the same species, I investigated this individual anatomically without making full notes on its external characters. It was, however, rather shorter and of less breadth, while the anterior narrower region of the body widened out to the full dimensions rather sooner than in the larger specimen.

I have investigated the scolex by means of longitudinal sections only in the smaller specimen last referred to. The four suckers look directly upwards, their orifice being terminal in such sections. There is nothing remarkable that I could detect about their structure. They do not bulge to any extent from the sides of the scolex, and these sections show that the scolex is hardly, if indeed at all, wider than the immediately following strobila. The rudimentary rostellum is merely a hemispherical elevation lying between the suckers. There is no terminal pit of any kind and no hooks discoverable. The water vascular tubes extend into the rostellum. Of the larger specimen I only examined the scolex without destroying it. It is clear that the structure is the same in all the points mentioned above, but I am not able to report upon the water vascular tubes in this region.

The structure of the body-wall (text-fig. 80) also differentiates these two species from the *Inermicapsifer* whose anatomy has been described above. The principal difference lies in the much more marked layer of transversely running fibres which bound the cortical layer internally and the medullary parenchyma externally. This layer is very much the same—I think exactly the same—in both of the two individuals of this genus which I refer later to different species. It is composed of very delicate fibres; but the layer, as a whole, is rendered more conspicuous by the fact that large fibres belonging to the longitudinal layer occur between the transversely running fibres. The cortical parenchyma is nearly as thick as the medullary. The stout longitudinal fibres which run in the former are to be found in the greatest numbers at about the middle of the cortical layer, but they occur elsewhere. They are not massed into large bundles, but two or three are here and there closely associated. This massing of the longitudinal fibres is not obvious in the larger specimen.

The *excretory vessels* consist of the usual dorsal and ventral tubes running continuously through the strobila. Anteriorly there is less difference in the calibre of these tubes than posteriorly. The position in relation to each other also becomes altered. In immature segments (where I have studied the excretory tubes) the rather smaller dorsal vessel lies obliquely above the ventral vessel to the

Text-fig. 80.



Hyracotænia hyracis.

Transverse section through a proglottid.

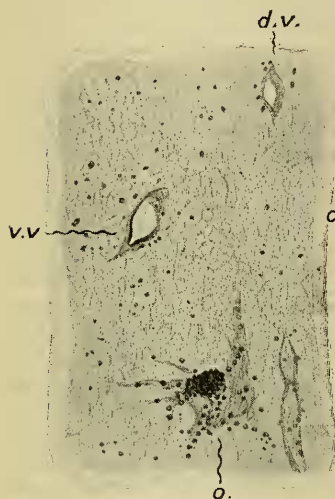
d.v. Dorsal excretory tube. *T.* Row of testes. *V.* Vitelline gland.
v.v. Ventral excretory tube.

pore side of the same. In maturer proglottids the two vessels are practically superposed, and the dorsal vessel is at times so minute as to escape observation. Both of these vessels are connected with a network of larger and smaller water vascular capillaries which traverse the medullary region of the body. I have seen branches of these ending in a testis, and it becomes a matter of

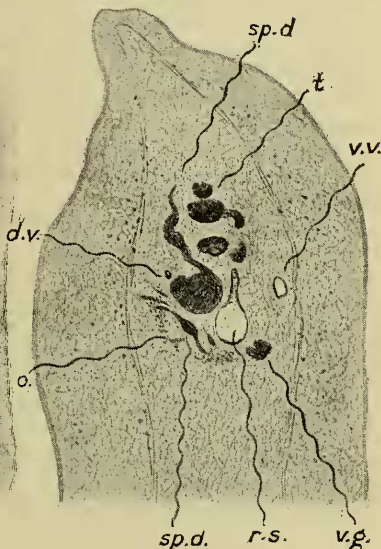
great interest to enquire if this network is directly connected with the network of vasa efferentia. But I have at present no further facts to offer.

The ovary of this tapeworm is unquestionably single. It lies on the pore side of each proglottid in the neighbourhood of the two longitudinal water vessels of that side. The ovary is apparently sometimes quite anterior to the testes, and sometimes is surrounded laterally by them. The vitelline gland is posterior to the ovary, which is thus the most anterior of the generative organs.

Text-fig. 81.



Text-fig. 82.



Text-fig. 81.—Part of a transverse section through a proglottid of *Hyracotænia hyracis*, to illustrate the immature ovary.

d.v. Dorsal excretory tube. *o.* Ovary. *v.v.* Ventral excretory tube.

Text-fig. 82.—Transverse section of one-half of a proglottid of the same species.

d.v. Dorsal excretory tube. *o.* Part of ovary. *r.s.* Receptaculum seminis. *sp.d.* Sperm-duct. *t.* Testes. *v.g.* Vitelline gland. *v.v.* Ventral excretory tube.

Its exact position with reference to the two water vascular vessels is not always identical. It is more dorsal or more ventral, as the case may be, and is sometimes entirely to the pore side of the ventral tube of the excretory system, and sometimes entirely to the median side of that tube; sometimes it extends to both sides. In any case it lies more or less between the dorsal and ventral excretory tubes. The ovary is not solid and compact, but arranged in a series of finger-like outgrowths radiating outwards and

dorsally. In young ovaries, such as the one figured in text-fig. 81, the riper eggs lie in straight lines connected by delicate threads with the central mass, and suggestive almost of the pseudopodia of a Rhizopod with the eggs carried along them. This radiating appearance of the ovary is retained until the organ is quite mature, when it consists of a group of sacs with, for the most part, definite walls, enclosed in which lie the ripe ova. I refer to this appearance of the ovary in considering the uterus on a later page. It seems possible that this condition of the ovary is to be compared to the testes, and that there are really several separate ovaries, which, however, are more closely adpressed than are the testes. In any case we have instances, like *Stilesia*, where the single ovary consists simply of a single mass of egg-cells, a condition which is to be compared with one of the subdivisions of the ovary in the present species.

The *vitelline gland* in the immature segments lies exactly opposite to the ovary, the vagina dividing, as described later, into two ducts, which end respectively in the ovary and vitelline gland. It is large and conspicuous in the mature proglottid. The *shell-gland* is also quite conspicuous in this tapeworm.

The *vagina* is wider and with thicker walls for a short space after its orifice on to the exterior. It then narrows and runs a very straight course towards the interior of the proglottid. It then becomes again wider, and opens gradually or abruptly into a dilated receptaculum seminis, which lies beside the vesicula seminalis. This region of the female duct is thin-walled. It is on a level with the ventral water-vessel. From the median end of the swollen receptaculum arise two tubes, one of them being the vitelline duct and the other the duct leading to the shell-gland and to the ovary. These two ducts are very much narrower than the receptaculum, into which they suddenly open. In immature proglottids the receptaculum is rather wider than the vagina, and gradually widens towards the internally situated end, there diverging into two horns which are respectively the vitelline duct and the ovarian duct. These ducts are in these immature segments of hardly less calibre than the end of the receptaculum into which they open. These and the sperm-duct pass towards the exterior between the dorsal and ventral water vascular tubes.

The terminal region of the vagina, *i. e.* that part nearest to the external orifice of the tube, has a lining which is very deeply stained by logwood, and so has the narrow region which immediately ensues; the rest of the vagina is not deeply stained in this way. I noticed in the larger of the two specimens which I report upon in the present communication that the narrow region of the vagina lying between the terminal part and the portion which may be termed receptaculum was much shorter than in the other example. I am not certain, however, whether there may not be some variation in this matter from segment to segment, an expansion of the lumen accounting for the different appearance. It

is certain, moreover, that the wide internal region of the vagina, before it divides into vitelline duct and ovarian duct, is susceptible to variation; for in some cases it was an abruptly formed spherical sac, at other times merely a wider tube than the immediately preceding region of the vagina. I mention later that the end of the receptaculum contains ripe ova in the mature proglottids. I have never seen spermatozoa therein.

Uterus.—In both of the two examples of this species the last few segments became somewhat shorter from side to side than those in front, and were also longer in the antero-posterior direction. One would naturally associate these changes in the facies of the proglottids with complete maturity and the existence in those segments of embryos. As I find in these segments completely ripe eggs quite detached from the ovary and associated together in small masses, I shall assume that the anatomical structure of these proglottids is that of complete maturity. In this case the present species differs from those which we have been considering by the entire absence of numerous paruterine organs like those of *Inermicapsifer*, etc. Even were these terminal segments not so fully mature as I presume them to be, there would be, I should imagine, at least some preparation for the formation of the paruterine organs. But there is none.

The ripe eggs were massed into more or less spherical groups surrounded by a membrane. These were not to be distinguished from the lobes of the ripe ovary, and I imagine that they were merely the persistent ovary. In addition to these masses of eggs, the end of the vagina, *i. e.* the dilated portion which I have termed receptaculum seminis, was found in many cases to be full or nearly full of ripe eggs unaccompanied by any interstitial cells. This was not only the case with a receptaculum which was swollen into a spherical contour at its base, but also in cases where the receptaculum ended merely as a slightly wider tubular sac. I have no reason whatever to doubt these facts, as the receptaculum is quite easy of identification. I am therefore disposed to think that there is no uterus as a distinct and separate structure, but that the eggs are partly voided into the receptaculum and partly remain *in situ* awaiting the loosening and perhaps disintegration of the proglottids. It may be that one of the rounded sacs which I regard as an ovary is really a uterus. Of this I cannot be positive, especially in view of the very few completely mature proglottids in both specimens. That both specimens were identical looks as if the conditions above described are to be regarded as normal.

The *testes* extend through a good part of each proglottid, and, as seen in sagittal sections, there are five or six rows of them laterally, though not so many in the median region. In transverse sections they are seen to extend from edge to edge of each segment, being nowhere interrupted save where they meet with the female reproductive organ. This row is mostly one deep, but in places two or even three deep. I counted from 40 to 50 or so of separate testes

in a single complete transverse series. There are thus altogether two or three hundred of these gonads to each mature proglottid. In more immature segments the testes did not appear to extend to the pore side of the longitudinal water-vessels but to stop short before quite reaching the median side of those vessels. In a mature segment I found that 44 out of the 50 sections which displayed it in its entirety were occupied by the testes, which thus fill up most of the segment, though the proportions were not always exactly as stated in the above instance. In proglottids from the other example of this species 3 sections without testes were followed by 15 sections showing testes, and these again by 5 without testes, and thereafter 14 with testes. It is therefore obviously the case that the testes occupy a great deal of the segments.

It will be observed that there is no grouping of the testes into two masses such as I have described in *Inermicapsifer capensis*. They lie mainly behind the ovary and vitelline gland, and in some proglottids the ovary lay rather more distinctly in front of the male gonads. The testes are more or less spherical or egg-shaped, and when ripe are seen to be surrounded by a layer of spermatozoa, which lie therefore, as I take it, in a cavity surrounding the testis, a cœlomic cavity. I never found the testes of this tapeworm to be pear-shaped, like those of *Inermicapsifer*. Furthermore, the testes, all of them, lie dispersed in quite unaltered parenchyma. As is very generally the case among the members of this group, the testes were mature much more anteriorly in the body to the ovary. It is, indeed, a striking feature of the present species, and one in which it contrasts, for example, with the species of *Inermicapsifer* that has just been described, that the mature testes occupy so many segments of the body, while the mature ovaries are so exceedingly limited in the number of segments in which they are found. The efferent tubules which collect the sperm form a very definite network (see text-fig. 83), which is copious and formed often of unequally sized vessels. A similar network has been described in other tapeworms, for example in *Chapmannia* *.

The *vas deferens* of this species (text-fig. 82, p. 597) is quite different from that of the species which we have already considered. The reticulate efferent ducts finally find their way into a large sac, which in the mature segments is stuffed with sperm, and which lies in the female generative mass alongside of the receptaculum ovarum. This large vesicula seminalis is flask-shaped, and therefore gradually narrows and emerges from the female generative mass as it passes towards the genital orifice. It is impossible to draw a hard-and-fast line between the vesicula seminalis and the sperm-duct proper with which it is continuous, for the gradual diminution in calibre of the entire tube forbids such a delimitation. The tube pursues a winding course, narrowing gradually and but slightly; it never forms an actual coil like the sperm-duct of so

* See Fuhrmann, Swedish Zool. Exped. Egypt, 1909, pt. iii.

many other—indeed the majority of—*Tetracotylea*, but is at most once or twice bent upon itself. It becomes very narrow for a

Text-fig. 83.



Portion of medullary region of a proglottid of *Hyracotenia hyracis*, to illustrate network formed by vasa efferentia (*v.d.*).

T. Testis. *tr.* Transverse muscular layer. *v.v.* Ventral excretory tube.

short distance in front of its opening into the cirrus sac. The course of the sperm-duct is roughly parallel to that of the vagina, with which it might be sometimes confused in those cases where the vagina has not so abrupt a transition into the receptaculum.

Along the course of the sperm-duct, which in ripe segments is gorged with sperm almost throughout, there lie masses of what appear to be prostatic cells, similar in the fact of their existence to those of *Inermicapsifer*, but different in appearance. In the present species these cells are of a clear, almost hyaline, appearance, which is possibly due to the state of their activity at the time when the worm was killed. In *Inermicapsifer capensis* and in the species which I originally named *Thysanotenia gambiana*, the prostatic cells were darkly staining and granular. Nevertheless, they appear to be equivalent structures in the two tapeworms. In sections where the sperm-duct appears in transverse section, these cells present the appearance of a winding duct cut transversely. This appearance is due to the clear cells clustered round the actual sperm-duct, which, as already said, is narrow of calibre close to where it opens into the cirrus sac, and thus not obvious in such sections. There can be no mistake, however, in transverse sections of proglottids, where the course of the sperm-duct is easily to be followed owing to its being filled with sperm.

In the second and larger individual there are certain definite differences in the form of the sperm-duct. The tube has no such great dilatation into a vesicula seminalis, and it is very much more coiled as it approaches the cirrus sac. It has, in fact, the large and close coil which is so typical of tapeworms. There is certainly nothing of the kind in the other individual. The clear cells already spoken of form a complete layer one cell thick round the mass of sperm in the sperm-duct, and are therefore, I take it, simply the epithelial wall of the sperm-duct. As the sperm-duct was in parts full of sperm, this difference cannot be owing, I believe, to the different stages of the maturity of the proglottids in this tapeworm as compared with those already described. It must, I think, be a specific difference, with which also, it will be observed, go differences in the position of the ovary and vitelline gland.

The *cirrus sac* of this worm is not at all large as in the allied forms comprised in the genera *Inermicapsifer* and *Zschokkeella*. It can be seen in sagittal sections to lie straight in front of the vagina close to the external aperture, and I have not noticed any genital cloaca. There is certainly nothing of any size, and in one section the penis was seen to protrude on to the exterior directly from the cirrus sac without any intermediate and common chamber. The cirrus sac is oval in form and surrounded, as is usual, by a strong layer of muscles. I could not see any indications of a flask shape such as is so common in tapeworms. In the interior of the sac are the usual nuclei belonging, it is to be presumed,

to delicate muscles which retract the cirrus. The latter was relatively wide and short and the sperm-duct within the cirrus sac not coiled. The protruded male copulatory organ reminded one rather of the penis of *Anoplotenia** than of a cirrus, for it was wider at the free end than just within the cirrus sac.

It is evident that this genus presents many resemblances to the genera *Zschokkeella* and *Inermicapsifer*†. It agrees with those genera in the following assemblage of characters:—The head is unarmed and the excretory tubules form a plexus, or at least a coil, at the very extremity of the rostellum, as in the species which has just been described; the segments are narrow and the genital pores are unilateral. The excretory tubules furthermore form a plexus within the medullary parenchyma throughout the body. The ovary lies to the pore side of the segments and is distinctly not a double organ; the vagina dilates into a wide receptaculum seminis. The cirrus sac, moreover, is small as contrasted with that of many other tapeworms. On the other hand, there are certain characters which argue against this placing of the worm whose anatomy has just been described. These are as follows:—The sperm-duct in our species is short and almost immediately dilates into a large and long seminal vesicle, a state of affairs which is not met with in the species of *Inermicapsifer* known at present. Finally, the network formed by the vasa efferentia is a feature hitherto unknown in the genus *Zschokkeella*, though it occurs in *Inermicapsifer*. Inasmuch as a reticular disposition of the vasa efferentia is not necessarily diagnostic of a given genus as far as we know, for it occurs in *Chapmannia lapica* and *Hymenolepis reticulata* and not in other (at any rate in some other) species of that genus, this fact alone would not perhaps necessitate the removal of the present species from the genus *Zschokkeella* to which other important characters would appear to assign it. But there is a negative character which may be of very great importance. In neither of the two individuals which I have studied was there the least trace of the formation of the characteristic “egg-capsules,” which I prefer for reasons already given to call paruterine organs.

In all the species of *Zschokkeella* and *Inermicapsifer* examined from this point of view, the formation of these capsules began perhaps rather far back in the body, but still a long way before the actual termination. Now both examples of the present genus in my possession ended posteriorly in a few segments which were rather longer than those preceding them and at the same time rather narrower, suggesting, in fact, the end of the body. They were, moreover, thicker than unripe segments. If this be not the completely mature end of the body, the worm would be very exceptional in the deferring of the egg-reservoirs to a point so very far behind the scolex. Besides, two specimens selected at

* See Beddard, P. Z. S. 1911, p. 1015, text-fig. 215.

† For the generic distinctions see below, p. 607.

random from the same host would hardly be likely to prove both abnormal in any way. Finally, we have in these segments rounded sacs with ripe eggs, though it must be admitted that these were eggs and not embryos. Some riper proglottids may, however, be missing; but even then the commencement of the paruterine organs would surely be visible.

It is therefore, as I think, impossible to include these worms in either of the genera with which I have just compared them. Of the remaining Anoplocephalidæ (to which family I think that these worms must be referred) there are only the genera belonging to the subfamily *Anoplocephalinae*. Of these *Cittotenia* and *Moniezia* need not be considered, since their generative apparatus is double in each segment. Of the remaining genera none agree with the two worms under consideration in all of the following points, viz., uterus at most inconspicuous, cirrus sac small, genital pores unilateral, ovary to pore side of proglottids, genital ducts pass between excretory vessels, testes posterior. I believe, therefore, that they must be referred to a new genus.

This new genus may be thus defined:—

Hyracotænia.

Scolex unarmed, with four unarmed suckers. Proglottids wide and very short, a little longer at extreme end of body, but always much wider than long. Genital pores unilateral, not borne upon papille. Cortical parenchyma thick, separated from medullary by a thin layer of circular fibres. Water vascular tubes four, dorsal and ventral, the latter larger, connected by a network of capillaries. Testes numerous, dorsal in position, lying behind and to sides of ovary; vasa efferentia forming a network; sperm-duct wide and sinuous or coiled; cirrus sac small; a short blunt wide penis protrusible. Ovary near water-tubes of pore side, single, in front of vitelline gland; dilated receptaculum seminis and very narrow vagina. Uterus small and sac-like; paruterine organs absent.

Hab. *Procavia capensis*.

It is not possible for me to distinguish definitely at present between generic and specific characters. The above embody characters usually considered in generic definitions. The two species may be, for the present at least, defined as follows:—

(1) *Hyracotænia procaviæ*, sp. n.

Length about 90 mm.; greatest diameter 5–6 mm. Body attains its greatest width about 25 mm. from anterior end. Testes very numerous. Sperm-duct rather dilated posteriorly, much coiled anteriorly. Ovary ventral, on outer side only or both sides of ventral vessel; vitelline glands dorsal. Vagina not greatly dilated posteriorly.

(2) *Hyracotænia hyracis*, sp. n.

Length about 70 mm.; greatest diameter 4.5 mm. Body attains its greatest width about 6 mm. from anterior end. Testes less numerous. Sperm-duct much dilated posteriorly, sinuous but not coiled anteriorly. Ovary more dorsal, to median side of water-vessels; vitelline glands ventral. Vagina usually much dilated posteriorly.

We now come to the consideration of the question of the possible identity of either or both of the above species with any of those enumerated from the Hyrax by Janicki. The only species of that series that can be considered (if, that is to say, there are really no paruterine organs in the forms described by myself) are *Tænia* (*Anoplocephala*?) *gondokorensis* of Klaptočz*, *Tænia* (*Anoplocephala*) *spatula* of v. Linstow†, and *Anoplocephala hyracis*, var. *hepatica* of Nassonow‡, termed *Inermicapsifer* spec.? by Janicki. Of these Klaptočz's species has a small scolex like the species described by me, but also an apical depression (?a rudimentary rostellum) which my species have not. Furthermore, the proglottids appear to be much smaller. In the species of v. Linstow we find too great a breadth, and the cirrus sac is too large for comparison with my species. The shape and proportions of Nassonow's species are like mine, but the scolex has a conical process. In all these species the details are insufficient.

There are thus in African animals—chiefly in Mammals (mostly in the Hyrax (*Procapra*), but also in Rodents and Lemurs), but extending to Birds (*Numida ptilorhyncha*)—a group of worms which show at least specific differences, but all of which have the following characters in common, viz., head unarmed and no neck, proglottids wider than long and as a rule very much so, genital pores unilateral, cirrus sac not very large, testes numerous, ovary not double. To these characters may possibly be added, if we exclude the species described above as *Hyracotænia* spp., or are led by further material to interpret their anatomy differently, the formation of numerous paruterine organs—or egg-capsules as they have been termed by others.

These characters (excluding the fate of the uterus) seem to me to necessitate the inclusion of this group of worms in the family Anoplocephalidæ.

The various species which agree in the foregoing characters cannot, however, on these alone be massed into one and the same genus without further consideration. If we subtract from the assemblage the species which I have described as *Hyracotænia procavia*, and which, as I think, must in any case be withdrawn from the group, the reasons for uniting the rest under a single generic name become more striking. For in this case all of the species possess paruterine organs of the same kind, unless, indeed,

* S.B. Wien. Ak. 1906.

† Jen. Zeitschr. Naturw. xxxv. 1901.

‡ Arb. Zool. Lab. Univ. Warschau, 1897.

Janicki be right in inferring that *Zschokkeella* really differs, a point which I have already gone into above (see p. 590). The description of a second species of *Zschokkeella** from a *Cercopithecus* does not throw any further light upon this particular matter. If it were not for the fact that *Davainia* seems in some of its species to possess paruterine organs of the same type, the African worms referred to might well be regarded as all congeneric, in which case, of course, *Zschokkeella* would have to be the name.

Janicki appears to me to be rather hard put to it to separate his *Inermicapsifer* from *Zschokkeella*. The differences are certainly small. As already stated, he relies upon supposed differences in the paruterine organs of which I am disposed to doubt the existence. He also mentions the thickness of the muscular walls in *Zschokkeella* as compared with *Inermicapsifer*, and a few other points which seem to me to be of minor importance and not even collectively as of generic rank. Janicki's comparisons are based chiefly upon his own account of *Inermicapsifer hyracis*, which was the only species investigated by him in a detailed fashion. I do not think that a further examination of other species referred to by Janicki will necessarily prove the identity of *Inermicapsifer* and *Zschokkeella* throughout. I would point out that my own account in the present paper of *I. capensis* shows some differences between that species and *I. hyracis*. These differences are mainly the posterior position of the genital pore, the existence of a vesicula seminalis, the complete separation of two groups of testes, and the presence of a rete mirabile along the course of the sperm-duct. Finally, the uterus is much more rudimentary in *I. capensis* than in *I. hyracis*. In some of these characters it would appear that *I. settii* agrees with my species and differs from *I. hyracis*. A further examination of these species may show that they agree in other characters not referred to by Janicki in his résumé of these forms.

I would reserve the generic name *Inermicapsifer* for these forms and refer "*Inermicapsifer*" *hyracis* to *Zschokkeella*. There now remains my genus *Thysanotenia*. Of that genus I have described two species which show many differences of structure. *Thysanotenia gambiana* is, as I now think, undoubtedly to be referred to *Zschokkeella*, with which it agrees in all points, if we may assume that the paruterine bodies are identical in the two. On the other hand, it will be, as I think, advisable to retain the name *Thysanotenia* for the second species of the genus (*T. lemuris*), which differs mainly in the following points:—There is no plexus of excretory tubes and the ventral vessel is very large, the dorsal being apparently absent in mature segments; the ventral vessels are connected in each segment by the usual transverse trunks; the receptaculum seminis is quite different from that of the other forms; the uterus

* *Z. remota*, see v. Linstow, Zeitschr. wiss. Zool. lxxxii. 1905.

is more rudimentary than in *Zschokkeella*. I should distinguish the various genera thus:—

- I. Excretory system forms a network in each segment. Receptaculum seminis long and forming end of vagina. Cirrus sac small.
- A. Genital pores median on edge of segment. Testes forming a continuous row. No vesicula seminalis. Uterus well developed at first *Zschokkeella*.
- B. Genital pores posterior on edge of segment. Testes in two groups. Large vesicula seminalis present. Seminal ducts form a network. Uterus never well developed.
Inermicapsifer.
- II. No excretory network. Receptaculum short and globular along the course of vagina. Cirrus sac rather large.
- A. Genital pores on conspicuous papilla. Testes forming continuous row. Uterus never well developed.
Thysanotaenia.

This arrangement is naturally only tentative, since we are at present in need of more information concerning the majority of the species already known from the Hyrax and enumerated by Janicki in the paper which has been so often referred to. There are also points in the structure of the species referred to the genus *Zschokkeella* which demand further investigation.

32. Additional Notes on the Living Specimens of the Australian Lung-fish (*Ceratodus forsteri*) in the Collection of the Zoological Society of London. By BASHFORD DEAN.*

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(Text-figures 84 & 85.)

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The two specimens of the Australian Lung-fish in the Zoological Society's collection have been living under unchanged conditions since 1898, *i. e.* about fourteen years. In this time they have been observed repeatedly by zoologists, whose interest in these important and rare batrachian-like fishes has led them, in several instances, to publish their notes in detail. There is still, however, much to learn about the habits of these fishes, and it is to be hoped that the opportunity will be seized generally to observe the present specimens, especially

* Communicated by the SECRETARY.